OBSERVATIONS ON THE DUAL CONTRACTION OF CRUSTACEAN MUSCLE[1]

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Crustacean skeletal muscle possesses characteristics of both smooth and striated muscles of vertebrates. Like smooth muscle, its inhibitory mechanism is peripheral rather than central (Richet, 1879). It does not respond so readily to single induction shocks as to repetitive stimulation. Under appropriate stimuli its contractions are sluggish, and maximal tonic contractions can be maintained for long periods without apparent fatigue (Richet, 1879). On the other hand, the muscle is cross-striated; is under voluntary control; and is capable of quick powerful contraction and prompt relaxation. As in vertebrate skeletal muscle, tonus, when present, is probably maintained through impulses passing to the muscle from its nerve (Barnes, 1930). The two types of response present such sharp contrasts that as a result of his studies on Astacus, Lucas (1917) concluded that the adductor muscle of the claw possesses two distinct neuro-muscular systems. He arrived at this conclusion mainly because of the break in the strength-duration curve of excitation associated with an abrupt change in the character of the muscular response. These two types of contraction so characteristic of crustacean muscle were the subjects of the present investigation.

EXPERIMENTAL

Experiments were made on the blue crab (*Callinectes sapsidus*), the spider crab (*Libinia canaliculata*), and the lobster (*Homarus*) under temperature conditions prevailing at the Woods Hole laboratory during the summer season. A claw-bearing appendage was removed and placed in a clamp. Stimuli were applied either to the nerve placed on non-polarizable electrodes or directly to the muscle by silver-silver chloride electrodes introduced through small openings in the shell. Induction shocks or condenser discharges were used to excite. Contractions of the adductor muscle were recorded either by attaching a lever directly

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to the muscle tendon or to the movable jaw of the claw, the tendon of the adductor being cut.

Single Brief Electrical Currents

Proceeding as above, single shocks were applied at regular intervals and intensity gradually increased from a subliminal value. Intervals were of sufficient length so that cumulative summation of effects of previous stimuli did not occur. Under such conditions, the quick contraction (twitch) always appeared first. As stimulus intensity was increased, the slow type of contraction appeared as a shoulder broadening the curve (Fig. 1*A*). If the time interval between stimuli is shortened, summation effects appear and the quick contractions are added to a slowly rising tonus wave (Fig. 1*C*). When the muscle was stimulated directly by a single condenser discharge or an induction shock, the E.M.F. had

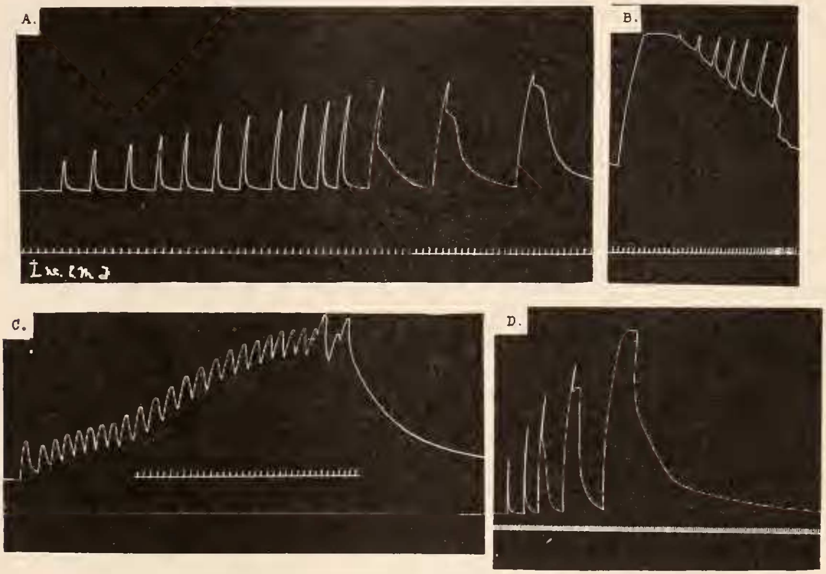

FIG. 1. *A*. Spider crab adductor stimulated directly by single condenser discharges of increasing E.M.F. Time in seconds.

B. Same preparation as *A*. Weaker stimuli applied during relaxation of slow contraction.

C. Spider crab adductor stimulated directly by single condenser discharges. Quick contractions are superimposed on a slowly rising tonus. Time in seconds.

D. Spider crab adductor stimulated through its nerve by single condenser discharges. Fourth and fifth contractions show a slow contraction developing after the quick contraction is over. Time in seconds.

to be increased three or four fold before the slow contraction appeared. With further increase, the contraction became progressively prolonged and frequently lasted several minutes following a single strong stimulus. By a slow repetition of the stimulus, e.g., 1 per second, the contraction under light tension could be continued for more than 10 minutes without evidence of fatigue. During the relaxation of the slow contraction, twitches could be superimposed by applying appropriate weaker stimuli (Fig. 1*B*). Results were essentially the same whether the stimulus was applied to the nerve or directly to the muscle, except that the nerve rapidly lost excitability under strong stimulation and only responded briefly to the higher intensities used. At the prevailing room temperature (23° C.), the total time of the quick twitch was not especially different from that of amphibian muscle, being in the neighborhood of 0.1 second for *Callinectes* and 0.2 second for *Libinia*. The duration of the slow contraction was a matter of seconds. With strong stimulus, it continued to develop after the quick component was over (Fig. 1*D*).

Repetitive Stimuli

Repetitive stimulation introduces the possibility that various factors, such as summation, fatigue, refractory or supernormal phases, may modify the result. To give repetitive stimuli, a motor-driven rotating double key was arranged to act as a charge-discharge key for condensers or to deliver make or break induction shocks as desired. The rate of stimulation was controlled by motor speed and reducing gears. By this means stimuli of varying frequency and intensity could be applied as desired. The determination of threshold, by this method, applying repetitive stimulation for brief periods, reversed the results obtained with single shocks. At a frequency below a certain limit any effects observed were those of single stimuli but if an intensity was chosen which was subliminal for the single stimulus and applied repetitively, the slow contractions appeared at the lower rate (Fig. 2*C, D*) to change to the quick type as frequency or intensity was increased. This change from slow to quick contraction was an abrupt one and not a gradual shortening of the contraction time. The frequency at which the abrupt changes appeared varied with the intensity of the stimulus and the condition of the preparation. This is in agreement with the results obtained on other crustacea by Blashko, Cattell, and Kahn (1931), and by Pantin (1936). Changing the procedure, the intensity of the stimulus was varied at different fixed frequencies. The results were essentially the same as above, i.e., the slow contraction appeared at the lower threshold (Fig. 2*E*). At very low frequencies a limit was reached where, if intensity was sufficient, effects were those of single stimuli and quick contractions appeared either singly or as saw-toothed notching on a slowly rising tonus contraction (Fig. 2*A*). With frequencies around 10 per second or higher, the slow contraction always appeared first as intensity was increased from subliminal values and changed to the quick type with further increase of intensity. On slow contractions as they developed or relaxed, quick contractions could be superimposed by application of single stimuli of proper intensity or by brief repetitive stimuli of greater strength or frequency.

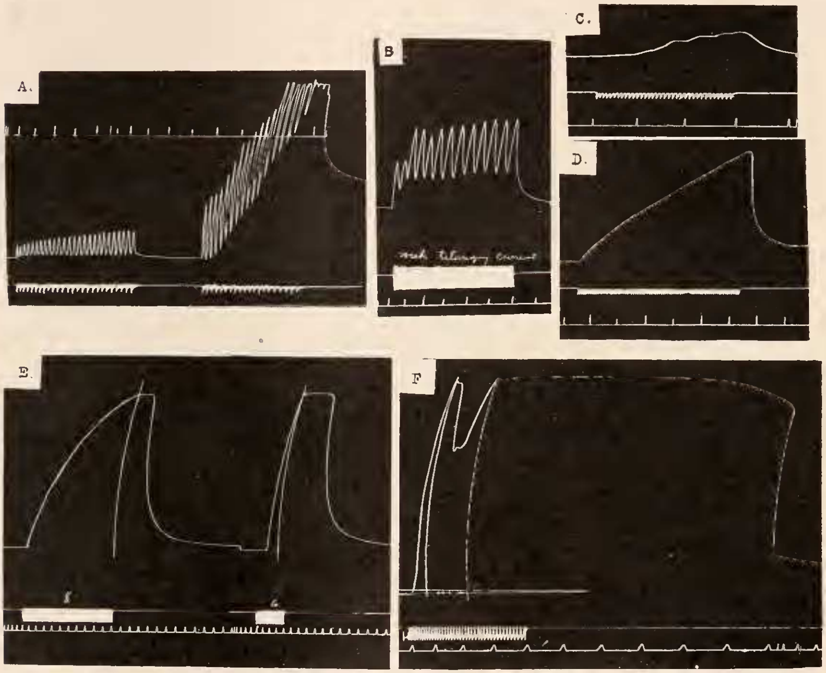

FIG. 2. *A*. Blue crab adductor stimulated by increasing intensity of repetitive induced currents (Harvard induction coil). Signal indicates stimulation frequency (4 to 6 per sec.). Time = sec.

B. Rhythmic quick contractions of lobster adductor stimulated directly by weak tetanizing current (vibrator). Time = sec.

C. Spider crab adductor stimulated at rate of 11 per sec. The slight irregularities are due to variations in output of stimulator. Signal indicates stimulation frequency. Time = sec.

D. Same preparation as *C*. Stimulation rate 14 per sec. Time = sec.

E. Blue crab adductor stimulated repetitively (vibrator) through its nerve with secondary induction of coil at 8 cm. and 6 cm. Lines drawn from crests of the curves indicate differences in time of slow and quick contractions. Time = ⅕ sec.

F. Blue crab preparation as in *E* shows the development of quick and slow contractions in the same curve. Strong stimulus. Time = ⅕ sec.

An especially interesting phase of response to repetitive stimulation was the frequent appearance of rhythmic twitches superimposed on the slow contraction. This rhythm when it appeared was quite independent of the frequency of stimulation. These rhythmic contractions appeared at stimulation intensities near the threshold and they often persisted with quite uniform rhythm during the period of stimulation (Fig. 2*B*). It was suggested by Knowlton and Campbell (1929) that they may be due to simultaneous excitation of inhibitory fibers or nerve endings.

Discussion

These experiments show that either the slow or the quick contraction may be excited selectively or both types may be excited simultaneously. When they are excited simultaneously the function of the slow contraction is to maintain the tension developed by the quick contraction. Bronk (1932) has presented evidence that it is the function of the slow contraction to maintain tension with less expenditure of energy associated with a slower rate of nerve discharge. As noted above, this tension can be sustained for a long time without evident fatigue.

With single stimuli of moderately short duration, such as induction shocks or condenser discharges, the quick contraction is elicited at a much lower threshold. With repetitive stimulation it requires greater frequency or intensity. Time relations are not unlike those of the twitch of amphibian muscle. On the other hand, in contrast to these characteristics, the slow contraction with its longer chronaxie or excitation time, has a much higher threshold for single stimuli, except for constant currents of long duration (Lucas, 1917). It is excited by repetitive stimuli of either lower frequency or intensity. With increasing strength of stimulation above the threshold, the contraction becomes more and more prolonged and may persist for some minutes after the stimulus has ceased.

The two types of contraction exhibited by crustacean muscle are so divergent in their characteristics that they suggest that they may be due to different muscle fibers. This was the conclusion arrived at by Lucas (loc. cit.). Indeed this possibility has not been entirely excluded. However no corresponding differences in the fibers of a given muscle have been observed, nor have differences in the innervation of the fibers composing any single muscle been described. It seems more probable that each fiber is capable of responding differently as frequency and possibly other charasteristics of the excitatory nerve impulses differ. In the evolution of muscle, smooth muscle with its sluggish contraction appears first. With the development of cross striation, ability to rapidly contract and relax appears. More primitive striated muscle like that of crustacea normally exhibits both types of contraction. In normal skeletal muscles of certain vertebrates such as those of the frog (*Rana temporaria*), the slow contraction (contracture) may still be elicited by appropriate stimuli (Bremer, 1932). Bremer's records of contracture in amphibian muscle find remarkable parallels in the records from crustacea presented in this paper. Such contractures are not the operation of a special contractile mechanism but the expression of a specific type of excitation of the muscle fibers (Bremer). Methods of excitation are generally similar to those causing slow contraction of crustacean muscle. In mammals no contracture has been shown to function in the normal movements of the body though contractures may appear under abnormal and pathological conditions as in certain myopathies or following the section and subsequent degeneration of a motor nerve. These contractures have been reviewed in detail by Gasser (1930). Thus slow contraction is found in all types of striated skeletal muscle. It is a normal mechanism in crustacea but vestigial in mammals. Its specific type of excitation is characterized by the slowness of its development and disappearance. Its long chronaxie requires a single stimulus of long duration (Lucas, 1917) or excessive strength or stimuli of lower intensity or duration applied repetitively so that they produce their effect by summation.

It seems entirely probable that the single stimulus of high intensity acts by setting up a repetitive effect in nerve fibers or nerve terminals. It is not possible to eliminate such effects by curare, since motor endings in crustacea are not paralyzed by curare (author's observation). Verzar and Ludany (1929) observed rhythmic electrical discharges from passage of a constant current through crustacean nerve. Barnes (1930) also noted that a repetitive nerve discharge was set up by strong stimulation as cutting or crushing, and Van Harreveld and Wiersma (1936) recorded repetitive action currents in the nerve associated with the slow contraction. Whatever its nature, the excitation process resulting in the slow contraction is characterized by remarkable powers of summation. Stimulation, even if subliminal, sets up persistent changes which are additive. Contraction may appear only after 40 or 50 separate stimuli extending over a number of seconds. It is this persistence of effects and their consequent summation which explains the selective effectiveness of repetitive stimulation for excitation of the slow contraction. On the basis of evidence at hand, it seems probable that the slow contraction of crustacean muscle can occur only as the result of stimuli which are repeated and summed.

The slow development and disappearance of this additive excitatory effect make it intriguing to consider the possibility that a humoral mechanism is involved. Many of its characteristics, especially its time relations, could be satisfactorily explained on this basis. Among the known humoral agents of vertebrates, adrenalin causes contraction of crustacean muscle (Du Buy, 1935). Pituitrin (vasopressin) also causes contraction and these contractions are of the slow type (author's observation).

As different frequencies selectively excite different types of contraction, these frequencies could be transmitted by one nerve fiber and it is not necessary to postulate multiple excitatory innervation though this possibility is not excluded. In a series of papers, Van Harreveld and Wiersma (1936–1939) have presented evidence that innervation varies in different crustacea. Examples of single, dual, triple, and even quintuple innervation are described. Even the different muscles of the same individual differ in mode of innervation (Van Harreveld 1939). Multiple innervation furnishing exclusive paths for different activities appears to possess distinct advantages over a single common path though it is not a necessity nor is it uniformly present.

Summary

The slow and quick types of contraction of skeletal muscle of certain crustacea have been investigated and characteristics of the two types of contraction are described. These contractions are correlated with "twitch" and "contracture" of vertebrate muscle.

By appropriate stimuli, one may excite either type of contraction selectively or may excite both simultaneously. When both types are produced by a single strong stimulus, the slow contraction functions to sustain and continue the tension developed by the quick contraction.

Due to the remarkable powers of summation associated with excitation of the slow contraction, it is most easily excited by repetitive stimuli of low intensity. Possibilities of a humoral factor are suggested.

On such a slow contraction, quick contractions may be superimposed by sudden increase of frequency or intensity.

Thus by appropriate stimuli one may excite either type of contraction selectively or may excite both simultaneously.

The function of multiple innervation is discussed briefly.

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